

On a New Species of Pentastomid from a N.
African Snake (*Zamenis ravigieri*).

By

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With 5 Text-figs.

THE specimens of Pentastomid described in this paper were given to me in the spring of 1913 by Mrs. Pixell Goodrich, who obtained them from the body cavity of *Zamenis ravigieri* while studying the hæmogregarine of that snake in the Sahara.

My thanks are due to Mrs. Goodrich for placing the material at my disposal and I should also like to take this opportunity of acknowledging my indebtedness to Dr. Marett Tims for his kind advice and encouragement.

There were two specimens, one ♂ and one ♀, the former being about 10 mm. and the latter about 40 mm. in length. I showed the ♂ to Dr. Sambon who believed it to be identical with a new species he had recently described¹ from *Bitis gabonica* and *B. arietans* under the name of *Porocephalus boulengeri*, and for which he proposed to create a new genus *Raillietia*, characterised as follows: "A bifid posterior extremity, three vesicular prominences round each hook-pit, the female sexual opening at the anterior end of the body."

On investigation of the internal anatomy of the African specimens, I found considerable differences of arrangement as compared with species hitherto described, the variation

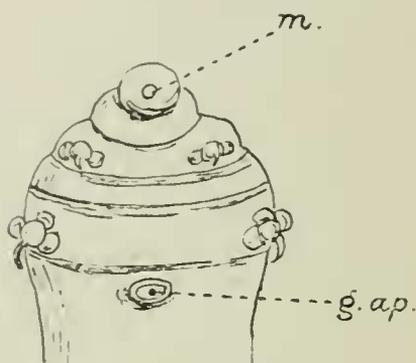
¹ 'Trans. Trop. Med.' vol. iii, 1910, p. 40.

being especially noticeable in the reproductive organs. These differences of internal structure, combined with the external features quoted above, appear quite sufficient to justify the establishment of the new genus.

EXTERNAL FEATURES.

The ♂ is 10 mm. the ♀ 40 mm. in length. In both cases the posterior extremity is bifurcated and the anterior end is almost triangular in shape. The cephalothorax is distin-

TEXT-FIG. 1.



Cephalothorax. *m.* Mouth. *g. ap.* Genital aperture.

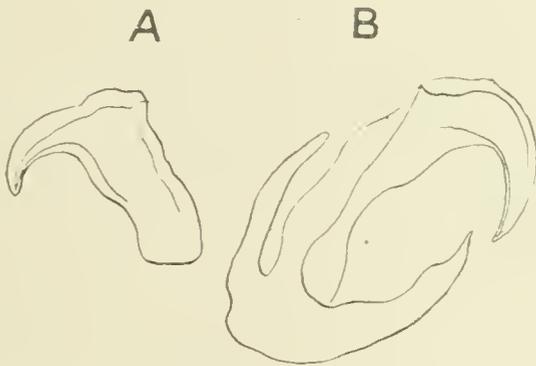
guished by the prominences which surround the hooks and mouth. The latter lies at the base of a circular depression on the ventral side of a large protuberance situated at the extreme anterior end of the cephalothorax (Text-fig. 1).

The hooks are simple and sharply curved, one pair lying in front of the other, and rather nearer to the middle line. The anterior hooks measure 26 mm. in length, the posterior 32 mm. (Text-fig. 2). Each hook is surrounded by three protuberances, one anterior and two lateral, those of the posterior pair of hooks being much more conspicuous than those of the anterior pair.

The annulation is difficult to determine. In the ♀ specimen the rings are practically obliterated; in the ♂ there appear to be about fifty body rings. In Dr. Sambon's species the annulation was indistinct, but he believed the rings to

number twenty-five to thirty.¹ In addition to the individuals described in this paper, I have had the opportunity of examining fourteen others (12 ♀, 2 ♂), obtained from African snakes which have died in the Zoological Society's Gardens, and apparently belonging to the same species. The rings were in nearly all cases distinct, and in the females numbered from thirty to forty. One of the males had thirty, the other thirty-five. It is quite possible that the number of rings for the male, given above as fifty, may be an error, since the body contracts in such a way as to make each ring appear

TEXT-FIG. 2.



Hooks. A. Anterior. B. Posterior.

double, but the mistake cannot now be rectified, as the specimen has been sectioned. Thus the number seems to vary between thirty and forty, in most cases being less than forty. These figures refer to body rings only, that is to say, rings behind the cephalothorax, which, however, is not clearly marked off in this species. I have regarded it as extending to and including the posterior pair of hooks. There are in addition three or four rings on the cephalothorax, well-marked, and nearly as wide as those on the body.

The anus opens between the two caudal processes.

The genital aperture is anterior both in the ♂ and ♀, and lies just behind the cephalothorax in the mid-ventral line, opening in the centre of a rounded papilla (Text-fig. 1).

¹ Loc. cit., p. 132.

In both specimens the integument was semi-transparent, so that the internal organs could be seen through it in places. A dark streak was observable in both, extending almost from end to end. This proved to be the contents of the intestine showing through the thin wall.

INTERNAL ANATOMY.

Alimentary Canal.

The mouth opens on the papilla before mentioned. Here the epithelium is considerably thickened and contains a number of gland-cells. The mouth-cavity is fairly large and lined with a deeply staining cuticle continuous with that of the external body layer. A mass of tissue projects into it from the roof, and is pierced by the pharynx. This leads upwards and backwards from the mouth-cavity, and is lined with similar cuticle, thin at first, but soon becoming thicker, especially on the posterior wall, which bulges out into the pharynx, making the lumen a narrow crescent-shape in cross-section, the horns pointing ventrally. Posteriorly the cuticle thins again. In the female a single layer of columnar epithelium can be seen beneath the cuticle, except just below the bulge of the posterior wall, where it is stratified, forming a thick mass. There is also a little mass of stratified epithelium in the anterior wall just opposite.

The pharynx becomes almost triangular in section at its posterior end, and then passes into the œsophagus.

The œsophagus is a dorso-ventrally compressed tube lined by a single layer of columnar epithelium. The cuticular layer is continued throughout, but is thinner and not so deeply staining. About halfway the œsophagus gives off a narrow dorsal diverticulum, and then becomes almost circular in outline. Finally it meets the antero-ventral wall of the intestine, into which it opens through an inwardly-projecting papilla.

The intestine or mid-gut extends from a point shortly in front of the posterior end of the œsophagus to the caudal end of the body. It is a relatively wide tube, which gradually

decreases in size posteriorly, and terminates in a very narrow rectum leading to the anus. The gut wall is composed of muscle layers, within which is a single layer of epithelium. This is not folded to any extent, as described in other species, but many of the cells are considerably elongated and produced into finger-like processes which project into the gut lumen. This is particularly noticeable in the female on the ventral side, and in both specimens the epithelium is much thickened in this region, especially in the posterior half of the body. The gut epithelium is characterised by its extremely glandular nature, especially in the thickened portions. The cells are crowded with a glandular secretion, which is extruded in little spherical masses to the gut lumen, where they are found in large numbers. In the male there are apparently a pair of lateral diverticula given off in the mid-region of the intestine, but this may possibly be due to shrinkage, as all the walls are thin and delicate and consequently liable to collapse.

The gut contained a large quantity of blood from the host in various stages of digestion, while a considerable number of hæmogregarines and of the granules mentioned above were found distributed through the mass of blood débris.

Secretory System.

Stigmata are present, but not very numerous.

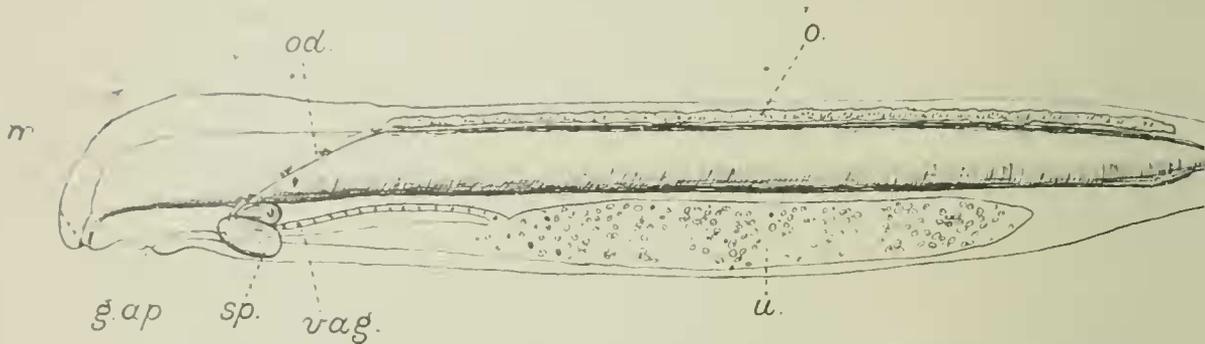
The head, hook, and parietal glands differ in no important respect from those of other species. The head and hook glands are not very clearly marked off from one another, and the latter are comparatively small, only stretching back for about a quarter of the length of the body. Parietal glands are present, and there is a certain amount of glandular tissue round the dilator-rod sac in the male and round the spermathecæ in the female. In addition to these there is in both sexes a glandular mass with very large cells lying dorsal to and partly enclosing the pharynx. It appears to be part of the head gland, and disappears where the pharynx passes into the œsophagus.

Nervous System.

The nervous system is typical. There is a large bilobed mass lying below and partly enclosing the œsophagus.

Near its anterior end it gives off a commissure which encircles the latter organ. The mass is obviously paired, and divides posteriorly into two separate halves for a short distance. The two halves then gradually approach again in the middle line and unite. Beyond this point they again diverge, and are continued backwards as two fairly stout nerve strands, rather wide apart and extending nearly to the

TEXT-FIG. 3.



♀ reproductive organs. *g.ap.* Genital aperture. *m.* Mouth. *o.* Ovary.
od. Oviduct. *u.* Uterus. *vag.* Vagina.

posterior end of the body. A series of paired nerves are given off from the sub-œsophageal mass to the muscles and papillæ.

Reproductive Organs.

Female.—The female reproductive system differs in several respects from any species of *Porocephalus* hitherto described.

The ovary is quite typical, and extends through the greater part of the body, lying dorsal to the intestine (Text-fig. 3). It is visible through the body wall as a narrow brown band, the colour being due to the outer egg-envelopes, which are here thick and of a deep reddish-brown. In section the ovary shows a structure much like that figured by

Spencer,¹ viz., a central tube, on the sides of which the ova are developed, forming two projecting lateral masses. The wall of the ovary is, however, unilaminar throughout except just at the base of the mesentery, and there is no trace of the dorsal syncytium or "lateral crests" described by Spencer. The cells of the ventral wall are somewhat columnar, and those of the dorsal wall are rounded and not clearly marked off from one another. The mesentery which connects the ovary with the dorsal body wall is median and unpaired. It is very narrow, and composed of fibres and connective tissue cells, with a small aggregation of the latter just at the point where it leaves the wall of the ovary.

The eggs in the ovary are relatively large and occur in various stages of development. Anteriorly the ovary passes into a rather wide oviduct with a similar histological structure. It is unpaired and found on the left side only, leading forwards and downwards round the intestine. I was unable to detect any traces of a right oviduct, either in the sections or in the dissection of another mature female specimen.

The duct is distended at intervals by batches of eggs making their way from the ovary to the uterus, and single ova may be seen at intervals in the lumen of the ovary itself. At its lower end the oviduct turns backward in the mid-ventral line and becomes much enlarged. The wall is here composed of columnar cells with a thin internal cuticle and an outer layer of circular muscles. The duct narrows somewhat and is joined by a pair of ducts from the spermatheca, one on each side.

The spermathecae are paired egg-shaped structures extending backwards on either side of the ventral median line. A short and comparatively wide duct leads from the anterior end of each spermatheca to the oviduct. The whole structure is like that described both by Leuckart² and Spencer (*loc. cit.*), except that the papilla through which the duct opens into the spermatheca is almost entirely in-

¹ 'Quart. Journ. Micr. Sci.,' vol. 34, 1892, p. 1.

² 'Bau u. Entwicklungsgeschichte der Pentastomen,' Leipzig, 1860.

vaginated into the spermathecal lumen. Also the histological structure of the spermathecal wall is somewhat different. There is no columnar epithelium to be seen at any point, but there is an internal layer of rather flattened epithelial cells with an outer muscular sheath. Apparently there is no cuticular lining. The epithelium appears slightly glandular in places especially on the outer wall, and, as already mentioned, there is a definite glandular mass apposed to the dorsal wall of each spermatheca. Both the spermathecæ were full of ripe spermatozoa. Accessory glands are present, and as in *P. tænioides*¹ they appear as forwardly pointing diverticula from the anterior walls of the spermathecal ducts. These latter and the accessory glands have a similar histological structure to that of the median oviduct; and they are all embedded in a glandular connective tissue, which is continued into the spermathecal papillæ. Posterior to the union of the spermathecal ducts the oviduct passes into the uterus.

The uterus (Text-fig. 3) runs backwards below the intestine and consists of three parts:

(1) A relatively narrow tube, just large enough to allow for the passage of one egg at a time. The eggs can be seen passing down it singly and separated by regular intervals. This duct in no way differs in structure from the median part of the oviduct. It soon passes ventrally into the uterus proper, the opening being marked by a ring of long columnar cells.

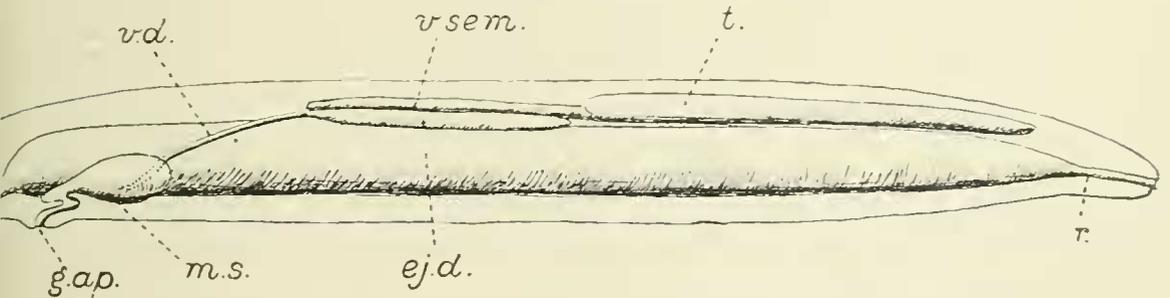
(2) The main portion of the uterus is extensive, being large and thin-walled, but not coiled. It occupies nearly half the body cavity, in some places pushing the gut to one side. The wall consists of a layer of very flattened cells with a thin cuticular lining. Outside this there appears to be a layer of circular muscle-fibres, but it is difficult to determine, as the whole wall is so attenuated. The uterus extends backwards and forwards from the union with the narrow tube, stretching from the spermathecæ nearly to the anus, and is crowded with

¹ Loc. cit.

embryos in different stages of development. Anteriorly it narrows to form the vagina.

(3) The vagina possesses a very thick cuticular lining, the innermost layer of which is deeply staining and produced into small processes. No radial striation is visible in the cuticle. The cells of the wall are columnar, with irregular outlines, and they are surrounded externally by a thick sheath of circular muscles. The cuticle does not extend right to the opening, but disappears shortly before this point. The vagina runs forward below the spermathecae in the middle line, widening again slightly and finally opening on the

TEXT-FIG. 4.



♂ reproductive organs. *ej. d.* Ejaculatory duct. *g. ap.* Genital aperture. *m.* Mouth. *m. s.* Muscular sac. *t.* Testis. *v. d.* Vas deferens. *v. sem.* Vesicula seminalis.

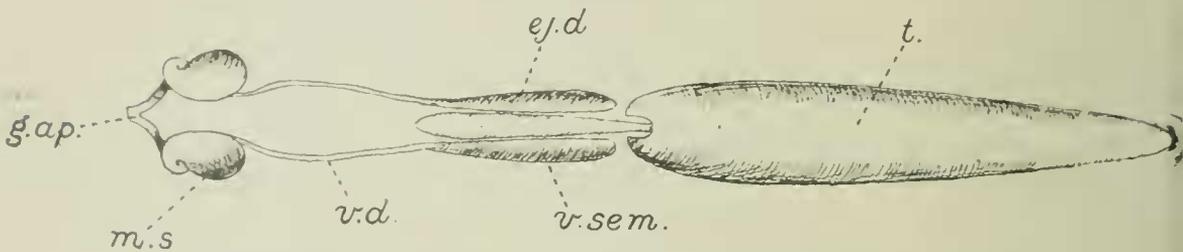
papilla mentioned above, just behind the posterior pair of hooks.

Male.—The male reproductive system is relatively simpler than in other species. It consists of two parts apparently unconnected. One comprises the testis and vesicula seminalis, the other the vasa deferentia, ejaculatory ducts, cirrus, cirrus bulb, dilator-rod sac, and common duct (Text-fig. 4).

The testis occupies the same relative position as the ovary in the female, and like it extends through the greater part of the body. It is a median, unpaired, tubular structure of considerable size, at its widest point occupying about a third of the body cavity. The thin outer wall is clearly distinguishable, but the inner syncytial layer has broken up into rounded masses. The whole testis is filled with spermatozoa

in all stages of development. Anteriorly it is produced into two forwardly-pointing lobes, between which runs a median structure, apparently the vesicula seminalis (Text-fig. 5). If such be the case, this organ is remarkable in being unpaired. The anterior end terminates blindly, and I could trace no communication between it and the vasa deferentia. It passes backwards for a short distance as a relatively wide tube, the structure of whose wall is like that figured by Spencer, viz., an inner layer of columnar epithelium with gland cells and an outer sheath of circular muscles, the whole being enclosed in a thin layer of connective tissue. The

TEXT-FIG. 5.



♂ reproductive organs seen from above. Lettering as in Text-fig. 4. The words *v. sem.* refer to the median structure.

diameter is nearly uniform until towards the posterior end, where it narrows considerably, and a little mass of connective tissue containing fibres begins to project inwards on the ventral side till it occupies half the cavity. In this projection a duct soon appears, whose wall consists of a single layer of columnar epithelium. As it passes backwards the dorsal half of the original lumen becomes filled with very glandular tissue, indistinguishable from that forming the inner wall of the testis, so that in this way the original cavity of the vesicula seminalis is altogether occluded. The whole structure becomes further reduced in size till only the ventral duct is recognisable, and this is gradually merged in the substance of the testis. From the position and structure of this median tube there seems little doubt that it represents the vesicula seminalis, though there were no sperms to be found at any

point in its course. There was a little coagulum observable in one or two places.

The vasa deferentia are paired. Each vas deferens is a narrow duct, terminating posteriorly on a level with the anterior end of the vesicula seminalis, dorsal to the intestine. No communication can be traced with the vesicula seminalis, but each vas deferens gives off posteriorly an ejaculatory duct which thus lies dorsal to the gut and lateral to the vesicula seminalis, with which it is practically co-extensive (Text-figs. 4 and 5). The vasa deferentia appear to be continued for a short distance into the ejaculatory ducts as narrow tubes lined with chitin, opening on a papilla into the lumen of the latter organs. The walls of the ejaculatory ducts consist of an inner layer of columnar cells with nuclei at their outer ends. These cells rest on a thin basement membrane, external to which is a layer of thick radial muscles. These are covered by a layer of connective tissue, the whole being enclosed in an outer sheath of very thin flattened cells. No cuticular lining was apparent.

From the junction with the ejaculatory ducts the vasa deferentia run forwards and downwards, encircling the intestine exactly in the same way as the oviduct of the ♀. At the lower end each becomes swollen to form a muscular bulb = the cirrus bulb which opens on the ventral side of a large muscular sac. In its passage down the side of the intestine the vas deferens runs on the inner side of this sac, lying between it and the intestine. The structure of the vasa deferentia is simple, the wall being composed of a single layer of columnar epithelium with large nuclei and a thin cuticular lining.

The muscular sac is a large structure with very thick walls and an internal chitinous lining. Anteriorly the wall is composed of enormously thick columnar epithelium, enclosing a fairly wide lumen, through which runs a small chitinous tube, apparently the cirrus. Farther back the lumen of this muscular sac becomes filled with muscular tissue, which gradually comes to occupy the whole cavity,

and the epithelial walls become indistinguishable. At this point the sac divides into two portions, the smaller ventral part forming the cirrus bulb, the larger dorsal part constituting the muscular sac proper. It is a little difficult to harmonise the conditions in this specimen with those found in other members of the group, but there seems little doubt that the muscular sac represents the dilator rod sac of other authors. Here, as in other cases, the walls, unlike those of the cirrus sac, are very thick and muscular, and there is a narrow semi-annular cavity lined with very deeply staining cuticle. From this there appears to project a small dilator rod connected with the cirrus. Further, the sac lies in the same position relative to the cirrus bulb and to the intestine as does the dilator rod sac. Anteriorly each sac is continuous with an S-shaped duct, whose course lies in the sagittal plane. Each duct passes forwards for a short distance, then bends back on itself ventrally, and finally takes another turn forward in the same plane. This backwardly turning loop seems to represent a rudimentary cirrus sac, and the cirrus cannot be traced forwards beyond this point. Anteriorly each duct bends inwards, and unites with its fellow of the opposite side in the ventral middle line to form a common genital duct opening by the genital aperture. The common duct is lined by a very thick, slightly staining cuticle.

The question arises as to whether the condition of the male reproductive organs is due to immaturity or whether the simplification is a distinguishing feature of the species or genus.

In favour of the view that it is immature we have the facts:

(a) That no sperms are to be seen in the vasa deferentia or vesicula seminales;

(b) that no communication could be traced between the vesicula seminales and vasa deferentia.

A similar condition to this last was described by Hoyle¹ for *P. protelis*. Stiles² suggests that the inability to

¹ 'Trans. R. Soc. Edin.,' xxxii, 1883, p. 183.

² 'Zeitschr. f. wiss. Zool.,' 52, 1891, p. 138.

find the communication in his specimen was due to the bad preservation of the material, as the duct is very small. On the other hand, *P. protelis* is an immature form, and Spencer¹ attributes the condition observed to this fact. As the two parts of the male reproductive system apparently arise independently the communication must be established later, and he suggests that at this period of development such communication has not yet taken place. In the specimen under discussion the condition might be due to either of these causes. The walls of the two ducts—viz., the vas deferens and the vesicula seminales—lie in close apposition at one point, and it is possible that a section may have been lost with the communicating passage, though it looks more as if the two walls were just in act of fusion and had not yet broken down.

Still even if not actually mature, the specimen cannot be far from maturity since some of the sperms in the testis are fully developed. Moreover, Leuckart states² that the first signs of spermatogenesis are coincident with the formation of the cirrus, and in the fully-formed larva of *P. proboscideum* Stiles³ describes the cirrus sac as already present when apparently spermatogenesis is only in its early stages. In our specimen spermatogenesis is far advanced and yet the cirrus sac is in a very rudimentary condition.

Hence the evidence seems to point to the conclusion that the specimen has almost reached sexual maturity, and the simplification of its parts must be regarded as a primitive feature. This simplification involves the straight or only slightly coiled cirrus, the slight development of the cirrus sac and the dilator rod, and the direct course of the vasa differentia comparable to that of the oviducts in the female. The median unpaired vesicula seminales may also be a primitive feature, but opinion on that point will differ according as to

¹ 'Quart. Journ. Mier. Sci.,' vol. 34, 1892, p. 1.

² 'Bau u. Entwicklungsgeschichte der Pentastomen.' Leipzig. 1860, p. 143.

³ 'Zeitschr. f. wiss. Zool., 52, 1891, pp. 131-135.

whether we regard the testis as paired or unpaired in origin.

When we consider the arrangement of the female reproductive organs the evidence in favour of a primitive condition is strengthened. It had already been noted by Leuckart that the reproductive organs in the two sexes are built on a fundamentally similar plan, that in the early stages of development they are indistinguishable and that it is only later that the peculiar features of the two systems can be recognised. In this case the adult male and female organs correspond more closely than usual. The paired vasa deferentia probably represent a more primitive condition than the single oviduct, but, however that may be, the oviduct is in a relatively similar position to the corresponding vas deferens, the latter encircling the intestine and passing from the dorsal to the ventral side instead of being entirely ventral as in other cases. Here it may be noted that Leuckart¹ describes a similar condition in the earliest stages of the development of the ♂ *Pent. taenioides*, the vasa deferentia being originally laid down in this position. It is not quite clear how they come eventually to lie entirely ventral to the intestine, but apparently they are carried downwards by the growth of the vesiculæ seminales with which they are bound up, although not in actual communication with them.

Another point of resemblance between the two sexes is the position of the genital opening. In other species the adult ♀ genital aperture is posterior, quite close to the anus, while in the ♂ it is anterior, lying close behind the last pair of hooks. In this specimen both the ♂ and ♀ genital apertures are anterior, which, according to Leuckart, is the original position, the two sexes being indistinguishable at first, when a pair of simple ducts (representing the future vasa deferentia or oviducts) pass down on either side of the intestine and open immediately below on a ventral papilla. This position is retained in the male, but in the female the aperture is carried

¹ 'Bau u. Entwicklungsgeschichte der Pentastomen,' Leipzig, 1860, p. 134.

back to the posterior end. Leuckart suggests that this is the result of a difference of growth of the body-wall in the two sexes, the male increasing in length entirely by growth at a point behind the genital aperture, the ♀ by growth entirely in front of it. In commenting on this, Stiles¹ remarks that if this is the case in *Pent. proboscideum* the change must have begun at a very early stage, as the difference of position of the apertures is obvious in the fourth week. But this would be in accordance with Leuckart's observations, since the shifting of the genital aperture would keep pace with the backward growth of the uterus, which begins very early. It would, therefore, seem most reasonable to accept Leuckart's suggestion and to consider the posterior position of the ♀ genital aperture as due to unequal growth of the body-wall, possibly brought about, in the first instance, by the backward growth of the uterus.

The arrangement in our specimen looks like a more primitive one, as the uterus has only grown back a short distance, forming a V-shaped tube, and the rest of the posterior extension consists of a very long diverticulum from the posterior wall. The uterus is here very thin walled, and instead of being a long, coiled structure it provides the necessary space by great development of the diameter of the diverticulum, which in some parts occupies half the body cavity, pushing the intestine to one side.

Thus, to sum up, apart from histological differences, this species differs from a true *Porocephalus* in the following particulars :

- (1) The bifid caudal extremity.
- (2) Anterior mouth opening.
- (3) Vesicular protuberances round the hooks.
- (4) A relatively lower degree of development in the ♂ genital system.
- (5) Unpaired vesicula seminales lying dorsal to the gut in the ♂.

¹ 'Zeitsch. f. wiss. Zool.,' 52, 1891, p. 141.

(6) Correlated dorsal extension of the vasa deferentia and dorsal position of the ejaculatory ducts.

(7) Uncoiled uterus in the ♀.

(8) Anterior position of the ♀ genital aperture with correlated differences of arrangement in the uterus and vagina.

Naturally the distinguishing features of the internal anatomy cannot be established as diagnostic characters without investigation of the other species referred to this genus, but there is little doubt that the general arrangement will be found to be the same, especially as in the ♀ it is partly dependent on the anterior position of the genital aperture, which is a constant feature for the genus.

I have no further remarks to add to those of Dr. Sambon on the specific value of *P. boulengeri*, but I should like to note that I have examined two other apparently undescribed forms of this genus—one from India, the other from S. Europe—of which I hope to give an account later. They both differ from *P. boulengeri* in quite small, but perfectly constant and recognisable details.

NOTE.—Since writing the above I have described the two new forms there mentioned in the 'Proceedings of the Zoological Society' for March, 1915.